

The genus *Salsola* (Chenopodiaceae) in southern Africa: Systematic significance of leaf anatomy

RR Klopper and AE van Wyk*

HGWJ Schweickerdt Herbarium, Department of Botany, University of Pretoria, Pretoria 0002, South Africa

* Corresponding author, e-mail: avanwyk@postino.up.ac.za

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Almost 90 species of *Salsola* L. are believed to occur in southern Africa. Correct identification of the different species is, however, rendered problematic by the great morphological similarity of almost all the species, uncertainties concerning the specific status of several entities and the unsatisfactory infrageneric classification of the group. A comparative anatomical study of the leaves of southern African *Salsola* species was conducted using LM and SEM techniques. The leaf anatomy of southern African *Salsola* species shows a variation on the typical Salsoloid-type Kranz-anatomy, in that the palisade mesophyll and bundle sheath are not continuous around the leaf, but only present abaxially. Leaf anatomy, particularly the structure of the leaf in transverse section and the type of the indumentum, proved

to be very useful for delimiting groups within the genus. The investigated species can be primarily divided into two main groups, according to the presence or absence of a uniseriate adaxial hypodermis. A secondary division can be made by using four main indumentum types, based on the appearance of the abaxial leaf surface. Species possessing one indumentum type can be further subdivided according to the area of the leaf covered by trichomes and the number of elongated cells in the trichomes. There is a weak association between leaf type and hitherto proposed subsections, as well as between leaf type and indumentum type. In general species possessing an adaxial hypodermis tend to have a denser indumentum than species lacking one.

Introduction

Salsola L. is one of the largest genera within the Chenopodiaceae (Cronquist 1981) with a fair proportion of more or less cosmopolitan species (Dyer 1975, Mabberley 1987). The genus is most conspicuous under semi-desert and desert conditions (Dyer 1975). *Salsola* is divided into seven sections, of which only one, section *Caroxylon* (Thunb.) Fenzl, is naturally found in southern Africa (Botschantzev 1969a, b). Leaves of *Salsola* are alternate, small and sessile. They are often succulent, covered with hairs and are usually densely packed, thus covering the branches (Solereder 1908, Dyer 1975, Hobson and Jessop 1975). The genus displays Kranz anatomy, which corresponds to the C4-type photosynthesis and specific habitat preference of *Salsola* (Solereder 1908, Metcalfe and Chalk 1979). However, its leaf anatomy shows a peculiar bundle sheath and therefore differs from the typical Kranz syndrome (Carolin *et al.* 1975, Carraro *et al.* 1993, Patrignani *et al.* 1993). Oxalic acid and salts of calcium, potassium or other minerals are commonly dissolved in the aqueous mesophyll cells of the group (Solereder 1908, Watt and Breyer-Brandwijk 1962). Members of the genus are also rich in sodium sulphate (Watt and Breyer-Brandwijk 1962).

There are 88 indigenous shrub species of section *Caroxylon* reported from southern Africa (Arnold and De Wet

1993). Two naturalised alien species of section *Salsola*, namely *S. kali* L. and *S. caroliniana* Walter, were also identified in the region (Botschantzev 1974c). The 88 indigenous species recognised by Botschantzev (1973, 1974a, b, c, d, 1978, 1981, 1983) are divided into three subsections, namely subsection *Caroxylon* (Botschantzev 1974d), subsection *Distichae* Botsch. and subsection *Tetragonae* (Ulbrich) Botsch. (Botschantzev 1972).

There are many taxonomic uncertainties within the southern African members of *Salsola* section *Caroxylon*. This is mainly due to the fact that the genus was initially not studied as an entity, but rather in the framework of the whole family, leading to the proposal of many artificial systems for the genus, that were almost all rejected. A further problem is that the majority of the work done on southern African members of the genus was done outside southern Africa with little or no fieldwork in the region. This is illustrated by the 69 species newly described from herbarium specimens by the Russian Victor Botschantzev (1910–1990) in St Petersburg. Hitherto very little taxonomic work had been done on the genus based on live plants and under natural conditions.

It is extremely difficult to distinguish between some of the proposed species of *Salsola* occurring in southern Africa, as they are morphologically very similar. The most recent key

available for the southern African species is that of Botschantzev (1974c). This key relies heavily on fruit and flower characters. These characters are, however, not always visible on herbarium specimens as *Salsola* species only flower briefly during favourable climatic conditions. This renders the key of very little practical value for routine identification. A further drawback is the fact that no less than 21 new species have been described (Botschantzev 1978, 1981, 1983) since the publication of this key. Furthermore, there exists great uncertainty as to the exact identity and taxonomic status of most of the 69 southern African *Salsola* species newly described by Botschantzev. Many species were described on the basis of very limited material and for 25 species only the type specimens are available (Botschantzev 1978). For this reason, many of these names have not been taken up and applied by southern African botanists.

Members of *Salsola* are of great agricultural, economic and ecological importance and are crucial components of Karoo vegetation. Because of the variable ecological and agricultural importance of different species of *Salsola* and the occurrence of harmful and beneficial species within the same area, correct identification of plants is of considerable importance. Therefore, the uncertainty as to the exact identity of most species described by Botschantzev is a major cause for concern, as it hampers research and management efforts where *Salsola* species are involved.

A clear delimitation of the different character states within the genus would greatly facilitate and enhance the process of solving the systematic problems that exist within the group. Botschantzev (1978) himself stated that the time has come to start the study of *Salsola* in southern Africa under natural conditions. Through this more material would be available for investigation. Thus it would be possible to delimit the species more accurately and to define their characters more precisely (Botschantzev 1978).

Botschantzev (1969a) places particular emphasis on two important characters to be used in separating groups within the family Chenopodiaceae and also for dividing *Salsola* into sections. These two characters are form (solid) and shape (outline) of the foliage leaves and trichome distribution. Therefore, anatomical and morphological characters of leaves may provide additional evidence to assist with the delimitation of infrageneric taxa in *Salsola*.

In this paper we report on a comparative study of the leaf anatomy in southern African members of the genus. Special emphasis is placed on the systematic significance of selected characters, notably the internal structure and indumentum of the leaves.

Materials and Methods

Material used in this study was either collected from plants in the natural habitat [voucher specimens deposited in the HGWJ Schweickerdt Herbarium (PRU), University of Pretoria] or obtained from herbarium specimens housed in the National Herbarium, Pretoria (PRE). Where available, mostly type specimens and specimens determined by Botschantzev were used due to the uncertainty that exists as to the exact identity of many species. Voucher specimens are listed in Table 1.

Fresh material was immediately fixed in a formalin-acetic acid-alcohol (FAA) mixture (Johansen 1940). Material from herbarium specimens was rehydrated by heating in distilled water and then fixed and preserved in FAA. For preparation of semi-thin sections, leaves were removed from stems with a sharp blade, dehydrated and embedded in the monomer mixture, glycol methacrylate (GMA), basically according to the method of Feder and O'Brien (1968).

Transverse sections, 3µm thick, were cut with glass knives on a Jung Multicut 2045 ultra-microtome. Sections were then stained with Schiff's reagent, according to the periodic acid-Schiff reaction (PAS) as proposed by Feder and O'Brien (1968) and counter-stained with 0.05% toluidine blue in benzoate buffer at pH 4.4 (Sidman *et al.* 1961). After staining, coverslips were applied to the dried slides with the mountant Entellan (Product 7961, E Merck, Darmstadt). A complete set of slides is housed at the Department of Botany, University of Pretoria. Photos were taken with an Olympus BH-2 microscope using Kodak Technical Pan film.

Leaf dimensions are given in millimetres in the order *length x width x thickness*. Cell proportions are given in micrometres as *anticlinal dimensions x periclinal dimensions*. Measurements are given as (*smallest measurement*–) *range* (–*largest measurement*). The range was calculated by subtracting and adding the standard deviation to the average and then choosing the measurements nearest to these calculated values. For all size calculations, at least ten measurements from each sample were used. Measurements were not made on specimens that appeared distorted due to poor rehydration.

To investigate trichome structure and length, epidermal peels of leaves fixed in FAA were made. The epidermal peels were stained with 0.05% toluidine blue in benzoate buffer at pH 4.4 (Sidman *et al.* 1961) for ± 1 minute. Stained material was mounted in distilled water and viewed with a light microscope.

For SEM study, material fixed in FAA was used. Samples were dehydrated using an ethanol sequence and thereafter critical point dried. Dried material was mounted on SEM plates with silver paint, sputter coated with gold and viewed and photographed with a Joel 480 SEM.

Results

Internal structure of lamina

Transverse sections show that two main leaf types can be identified, namely: leaves with an adaxial hypodermis and leaves without an adaxial hypodermis (Figures 1 and 2). These leaf types have been used as a primary division of the investigated species into two groups (Table 2). Detailed leaf anatomical descriptions for individual species are supplied by Klopper (2000).

Key to leaf types

Leaves with a uniseriate hypodermis underlying adaxial epidermis.....*Leaf Type H+*
Leaves without a hypodermis underlying adaxial epidermis.....*Leaf Type H-*

Table 1: Specimens of *Salsola* investigated. [Localities are given as quarter grid references (Edwards and Leistner 1971). Herbarium acronyms follow Holmgren *et al.* (1990)]

Species	Collector and number	Grid	Herbarium
<i>S. acocksii</i> Botsch.	Acocks 18809, Isotype	2819BB	PRE
<i>S. aellenii</i> Botsch.	Acocks 13198, Isotype	3119BD	PRE
	Geo Potts (Bloemfontein University 6613)	2926AA	PRE
<i>S. albida</i> Botsch.	Lang (sn 31718)	2723AD	PRE
	Leistner 2170, Syntype	2824BA	PRE
<i>S. aphylla</i> L.f.	Bohnen 8406	3321CC	PRE
	Burger 600	2427AB	PRE
	Collins 26	2722DD	PRE
	Giess 8310	2418AB	PRE
	Van Zinderen Bakker 1000	2827AC	PRE
<i>S. apterygea</i> Botsch.	Theron 1645, Isotype	3120BD	PRE
<i>S. araneosa</i> Botsch.	Dinter 4017, Isolectotype	2715BC	PRE
<i>S. calluna</i> Fenzl ex C.H.Wr.	RR Klopper & AW Klopper 33	3023DA	PRU
	Smith 5305, Holotype	2925AC	PRE
	Smith 5355	2925CB	PRE
	Verdoorn 2301	2925CB	PRE
<i>S. cauliflora</i> Botsch.	Giess 10311, Type	2516DD	PRE
<i>S. ceresica</i> Botsch.	Acocks 14455, Isotype	3219DA	PRE
<i>S. dealata</i> Botsch.	Acocks 17827	3124AB	PRE
	Acocks 17830, Isotype	3124AB	PRE
<i>S. decussata</i> C.A.Sm. ex Botsch.	Schlechter 8091, Isotype	3118DA	PRE
<i>S. denudata</i> Botsch.	Giess 8362, Isotype	2619CA	PRE
<i>S. dinteri</i> Botsch.	Dinter 4972, Isotype	2718CA	PRE
<i>S. etoshensis</i> Botsch.	De Winter 3610, Isotype	1915BB	PRE
	Van Son (sn 28789)	2419BD	PRE
<i>S. exalata</i> Botsch.	Henrici 3886b	2925AC	PRE
	Verdoorn 1599, Holotype	2924DB	PRE
<i>S. gemmata</i> Botsch.	Giess & Robinson 13221, Isotype	2514DB	PRE
<i>S. gemmifera</i> Botsch.	Dinter 4049	2715BC	PRE
	Dinter 6456, Isotype	2715DD	PRE
<i>S. giessii</i> Botsch.	Giess 3770, Isotype	2216DC	PRE
<i>S. glabra</i> Botsch.	Giess 9139, Isotype	2115BD	PRE
<i>S. glabrescens</i> Burt Davy	Burt Davy 1496, Isotype	2725DA	PRE
	Henrici 3909	2925CB	PRE
	RR Klopper & AW Klopper 188	3021BC	PRU
	Smith 3901	2925CB	PRE
<i>S. henriciae</i> Verdoorn	Henrici 3897, Holotype	3022CA	PRE
	Sidey 533	3022CA	PRE
<i>S. huabica</i> Botsch.	Giess 7947, Isotype	2014AC	PRE
<i>S. humifusa</i> A.Brückn.	Acocks H1282	2824DB	PRE
	Smith 4514, Holotype	2925AC	PRE
<i>S. inaperta</i> Botsch.	Story 5298, Syntype	1920DC	PRE
<i>S. kali</i> L.	RR Klopper & AW Klopper 164	3118DA	PRU
<i>S. kleinfonteini</i> Botsch.	Giess 8312, Isotype	2516BB	PRE
<i>S. koichabica</i> Botsch.	Merxmüller & Giess 28451, Isotype	2615BC	PRE
<i>S. marginata</i> Botsch.	Giess 8342, Isotype	2218CA	PRE
<i>S. melanantha</i> Botsch.	Leistner 1486, Isotype	2824BA	PRE
<i>S. merxmülleri</i> Aell.	Acocks 14228	2916BD	PRE
	Merxmüller & Giess 2289, Isotype	2615CA	PRE
<i>S. microtricha</i> Botsch.	Acocks 16291, Isotype	3125DB	PRE
<i>S. minutifolia</i> Botsch.	Coetzer 53, Holotype	3121DC	PRE
<i>S. okaukuejensis</i> Botsch.	Giess 15462, Isotype	1915BB	PRE
<i>S. patentipilosa</i> Botsch.	Acocks 13204, Holotype	3019CD	PRE
	Breuckner 1159	2623DB	PRE
	RR Klopper & AW Klopper 160	3118DA	PRU
<i>S. rabieana</i> Verdoorn	Breuckner 165	2824DA	PRE
	Herman 366	2924DD	PRE
	RR Klopper & AW Klopper 53	3021DB	PRU
	Verdoorn 2297	2925CB	PRE
<i>S. robinsonii</i> Botsch.	Giess & Robinson 13237, Isotype	2615CA	PRE
<i>S. scopiformis</i> Botsch.	Merxmüller & Giess 28891, Isotype	2618CA	PRE

Table 1 cont.

Species	Collector and number	Grid	Herbarium
<i>S. seminuda</i> Botsch.	De Winter 3257, Isotype	2618CA	PRE
<i>S. sericata</i> Botsch.	Acocks 19585, Holotype	3017BA	PRE
<i>S. smithii</i> Botsch.	RR Klopper & AW Klopper 57	3021DB	PRU
	Smith 5347	2924DB	PRE
	Smith 5439, Isotype	2925CD	PRE
<i>S. tuberculata</i> (Moq.) Fenzl	Henrici 4923	2925CB	PRE
	Pole-Evans 2245	2921AC	PRE
	RR Klopper & AW Klopper 179	3020AD	PRU
	Story 1109	2921AC	PRE
<i>S. tuberculatiformis</i> Botsch.	Acocks 14443	3319AD	PRE
	Leistner 3035	2721AD	PRE
	RR Klopper & AW Klopper 174	3019CD	PRU
<i>S. warmbadica</i> Botsch.	Acocks 18805, Isotype	2819DA	PRE
<i>S. zeyheri</i> (Moq.) Bunge	Acocks 13206	3019CD	PRE
	RR Klopper & AW Klopper 162	3118DA	PRU
	Zeyher 1447 (<i>planta alternifolia</i>), Isolectotype	3418AD	PRE

Description of Leaf Types

Leaf Type H+

OUTLINE in transverse section \pm semi-circular; \pm (0.78–) 1–2.08 (–3.58)mm x (0.55–) 1.07–1.75 (–2.7)mm x (0.3–) 0.5–1.2 (–1.87)mm, thickest at midrib; margin thinly to very thinly tapering. CUTICLE very thin ($>$ 1 μ m) to thin (\pm 2 μ m) adaxially; thin (\pm 2 μ m) to medium thick (\pm 4 μ m) abaxially. ADAXIAL EPIDERMIS uniseriate; periclinal cell walls longer than anticlinal cell walls, \pm (5–) 10–18 (–33) μ m x (15–) 23–38 (–64) μ m, cell size often decreases towards leaf margin; cell walls usually \pm equally thickened, outer periclinal cell walls sometimes thicker than inner periclinal or anticlinal cell walls, inner periclinal cell walls only rarely thicker than outer periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS uniseriate; periclinal cell walls usually longer than anticlinal cell walls, cells only rarely \pm isodiametric to anticlinal cell walls longer than periclinal cell walls, \pm (9–) 17–31 (–47) μ m x (15–) 23–39 (–65) μ m, cell size often decreases towards leaf margin; outer periclinal cell walls usually thicker than inner periclinal and anticlinal cell walls, cell walls sometimes \pm equally thickened. STOMATA paracytic; only occur abaxially (leaves hypostomatic) in area where palisade mesophyll and bundle sheath layers are present; mostly abundant, only sometimes rare; \pm sunken to not sunken; often with a thick cuticle; guard cells parallel to one another, pores arranged transversely to median vein of leaf. ADAXIAL HYPODERMIS present; uniseriate; cell walls lignified; often contain cubic crystals near inner periclinal cell walls. ABAXIAL HYPODERMIS present; uniseriate, rather weakly differentiated; cells \pm isodiametric, often contain cubic crystals. PALISADE MESOPHYLL present; uniseriate, placed abaxially; cells cylindrical, \pm (31–) 41–66 (–94) μ m x 5–10 (–17) μ m, cell size sometimes decreases slightly towards leaf margin. SPONGY MESOPHYLL present; cells large, thin-walled; cell size sometimes decreases towards leaf margin; cells adjacent to bundle sheath often contain cubic crystals. BUNDLE SHEATH LAYER present; comprising a single layer underlying palisade mesophyll; anticlinal cell walls usually longer than periclinal cell walls, cells sometimes \pm cubic, \pm (11–) 22–37 (–54) μ m x (11–) 16–27 (–45) μ m; cell walls

not thickened. VASCULAR BUNDLES one to many; main vascular bundle centrally placed, often closer to adaxial epidermis, usually with a large to very large sclerenchyma cap; secondary vascular strands several, small, associated with bundle sheath layer. INDUMENTUM TYPE 1, 2, 3a.i, 3a.ii, 3b.i, 3b.ii, 4a.

Species possessing Leaf Type H+ (Indumentum Type in brackets)

<i>S. acocksii</i> (3b.ii)	<i>S. giessii</i> (3b.i)	<i>S. rabieana</i> (3b.i)
<i>S. albida</i> (3b.i)	<i>S. glabrescens</i> (4a)	<i>S. robinsonii</i> (3b.i)
<i>S. aphylla</i> (3a.ii)	<i>S. huabica</i> (3b.i)	<i>S. scopiformis</i> (2)
<i>S. apterygea</i> (4a)	<i>S. kleinfonteinii</i> (3a.i)	<i>S. sericata</i> (2)
<i>S. araneosa</i> (1)	<i>S. koichabica</i> (3b.i)	<i>S. tuberculata</i> (3b.i)
<i>S. ceresica</i> (3a.ii)	<i>S. marginata</i> (3a.i)	<i>S. tuberculatiformis</i> (3b.i)
<i>S. dealata</i> (4a)	<i>S. merxmuelleri</i> (3a.i)	<i>S. warmbadica</i> (3b.i)
<i>S. etoshensis</i> (3b.i)	<i>S. microtricha</i> (3b.i)	<i>S. zeyheri</i> (1)
<i>S. exalata</i> (4a)	<i>S. okaukuejensis</i> (3b.i)	
<i>S. gemmifera</i> (4a)	<i>S. patentipilosa</i> (3b.i)	

Leaf Type H-

OUTLINE in transverse section \pm semi-circular; \pm (0.48–) 0.95–2.5 (–4.8)mm x (0.51–) 0.88–1.85 (–2.54)mm x (0.4–) 0.5–1.16 (–1.9)mm, thickest at midrib; margin thinly to roundly tapering. CUTICLE very thin ($>$ 1 μ m) to thin (\pm 2 μ m) adaxially; thin (\pm 2 μ m) to medium thick (\pm 4 μ m) abaxially. ADAXIAL EPIDERMIS uniseriate; periclinal cell walls longer than anticlinal cell walls, \pm (5–) 10–19 (–27) μ m x (18–) 24–39 (–59) μ m, cell size often decreases towards leaf margin; cell walls \pm equally thickened to outer periclinal cell walls thicker than inner periclinal or anticlinal cell walls. ABAXIAL EPIDERMIS uniseriate; periclinal cell walls usually longer than anticlinal cell walls, cells only rarely \pm isodiametric to anticlinal cell walls longer than periclinal cell walls, \pm (12–) 15–34 (–53) μ m x (15–) 21–42 (–63) μ m, cell size often decreases towards leaf margin; outer periclinal cell walls usually thicker than inner periclinal or anticlinal cell walls, cell walls sometimes \pm equally thickened. STOMATA paracytic; only occur abaxially (leaves hypostomatic) in area where palisade mesophyll and bundle sheath layers are present; mostly abundant, some-

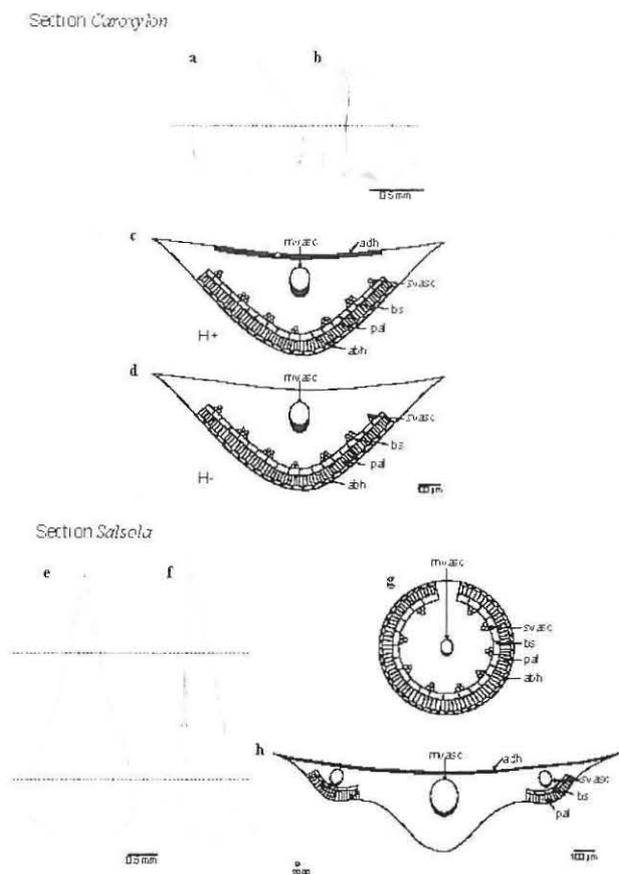


Figure 1: Diagrammatic representation of leaf types. **a–d** Section *Caroxylon*. **a** Abaxial view of leaf. **b** Lateral view of leaf. **c** Leaf Type H+. **d** Leaf Type H-. **e–h** Section *Salsola*. **e** Abaxial view of leaf. **f** Lateral view of leaf. **g** Section through tip of leaf showing Salsoloid-type Kranz-anatomy. **h** Section through base of leaf. Dotted lines indicate the position of the illustrated sections. **abh** – abaxial hypodermis; **adh** – adaxial hypodermis; **bs** – bundle sheath; **mv, asc** – main vascular bundle; **sv, asc** – secondary vascular tissue; **pal** – palisade mesophyll

times rare; mostly do not appear to be sunken, sometimes \pm sunken; sometimes with a thick cuticle; guard cells parallel to one another, pores arranged transversely to median vein of leaf. ADAXIAL HYPODERMIS absent. ABAXIAL HYPODERMIS present; uniseriate, rather weakly differentiated; cells \pm isodiametric, often contain cubic crystals. PALISADE MESOPHYLL present; uniseriate, placed abaxially; cells cylindrical, \pm (28–) 34–50 (–59) μm \times (4–) 6–10 (–14) μm , cell size sometimes decreases slightly towards leaf margin. SPONGY MESOPHYLL present; cells large, thin-walled; cell size sometimes decreases towards leaf margin; cells adjacent to bundle sheath often contain cubic crystals. BUNDLE SHEATH LAYER present; comprising a single layer underlying palisade mesophyll; anticlinal cell walls usually longer than periclinal cell walls, cells sometimes \pm cubic, periclinal cell walls only rarely longer than anticlinal cell walls, \pm (12–) 19–31 (–42) μm \times (11–) 14–24 (–35) μm ; cell walls not thickened. VASCULAR BUNDLES one to many; main vascular bundle cen-

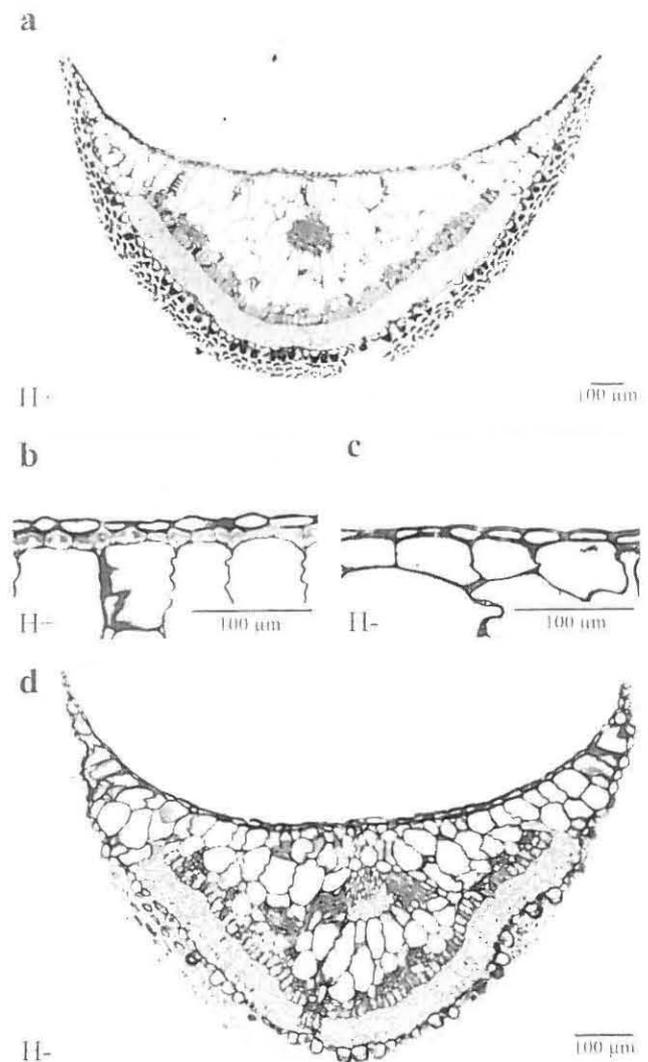


Figure 2: Leaf types. **a and b** Leaf Type H+. **a** Internal structure of leaf. **b** Adaxial epidermis with underlying hypodermis. **c and d** Leaf Type H-. **c** Internal structure of leaf. **d** Adaxial epidermis

trally placed, sometimes closer to adaxial epidermis, sometimes with small to large sclerenchyma cap; secondary vascular strands several, small, associated with bundle sheath layer. INDUMENTUM TYPE 2, 3a.i, 3a.ii, 3b.i, 4a, 4b.

Species possessing Leaf Type H- (Indumentum Type in brackets)

<i>S. aellenii</i> (4a)	<i>S. dinteri</i> (2)	<i>S. inaperta</i> (4a)
<i>S. calluna</i> (4b)	<i>S. gemmata</i> (2)	<i>S. melanantha</i> (3b.i)
<i>S. cauliflora</i> (3a.ii)	<i>S. glabra</i> (4a)	<i>S. minutifolia</i> (4a)
<i>S. decussata</i> (2)	<i>S. henriciae</i> (3a.i)	<i>S. seminuda</i> (4a)
<i>S. denudata</i> (4a)	<i>S. humifusa</i> (4a)	<i>S. smithii</i> (4a)

Leaf indumentum

Four main indumentum types can be identified on the basis of surface appearance (Figure 3). These indumentum types have been used as a secondary division (following leaf type)

Table 2: Summary of principal leaf anatomical characters in southern African species of *Salsola*

Subsection (following Botschantzev 1974c 1978; 1981; 1983)	I D Reliability	Species	Leaf type		Indumentum type								
			H+	H-	1	2	3a.i	3a.ii	3b.i	3b.ii	4a	4b	
C	1	<i>S. araneosa</i>	X		X								
C	1; 2; 3	<i>S. zeyheri</i>	X		X								
C	1	<i>S. scopiformis</i>	X			X							
C	1	<i>S. sericata</i>	X			X							
C	1	<i>S. kleinfonteini</i>	X					X					
C	1	<i>S. marginata</i>	X					X					
C	1; 2	<i>S. merxmuelleri</i>	X					X					
C	2; 3	<i>S. tuberculata</i>	X					X					
C	2; 3	<i>S. tuberculatiformis</i>	X					X					
C	3	<i>S. aphylla</i>	X						X				
C	1	<i>S. ceresica</i>	X						X				
C	1; 2	<i>S. albida</i>	X							X			
C	1; 2	<i>S. etoshensis</i>	X							X			
C	1	<i>S. giessii</i>	X							X			
C	1	<i>S. huabica</i>	X							X			
C	1	<i>S. koichabica</i>	X							X			
C	1	<i>S. microtricha</i>	X							X			
C	1	<i>S. okaukuejensis</i>	X							X			
C	1; 2; 3	<i>S. patentipilosa</i>	X							X			
C	1	<i>S. robinsonii</i>	X							X			
C	1	<i>S. warmbadica</i>	X							X			
C	1	<i>S. acocksii</i>	X								X		
C	1	<i>S. apterygea</i>	X									X	
C	1; 2	<i>S. dealata</i>	X										X
C	1; 2	<i>S. gemmifera</i>	X										X
C	1; 2; 3	<i>S. glabrescens</i>	X										X
C	2; 3	<i>S. rabieana</i>	X										X
C	1	<i>S. dinteri</i>		X		X							
C	1	<i>S. gemmata</i>		X		X							
C	1	<i>S. cauliflora</i>		X				X					
C	1	<i>S. melanantha</i>		X					X				
C	1	<i>S. denudata</i>		X								X	
C	1	<i>S. glabra</i>		X								X	
C	1	<i>S. seminuda</i>		X								X	
C	1; 2; 3	<i>S. calluna</i>		X									X
T	1; 2	<i>S. exalata</i>	X									X	
T	1	<i>S. decussata</i>		X		X							
T	1; 2	<i>S. henriciae</i>		X				X					
T	1; 2	<i>S. aellenii</i>		X								X	
T	1; 2	<i>S. humifusa</i>		X								X	
T	1; 2	<i>S. inaperta</i>		X								X	
T	1	<i>S. minutifolia</i>		X								X	
T	1; 2; 3	<i>S. smithii</i>		X								X	
S	3	<i>S. kali</i>	X									X	

ID Reliability: 1 = includes type specimen (listed in Table 1); 2 = includes specimen determined by Botschantzev; 3 = includes other specimen
 Subsection: C = *Caroxylon*; T = *Tetragonae*; S = alien species from Section *Salsola*

Leaf type: H+ = with adaxial hypodermis; H- = without adaxial hypodermis

Trichome type: 1 = trichomes long, round in transverse section, entangled; 2 = trichomes round to flattened in transverse section, slightly adpressed to almost entangled; 3a.i = trichomes flattened in transverse section, adpressed, consisting of one elongated cell, leaf margin glabrate; 3a.ii = trichomes flattened in transverse section, adpressed, consisting of more than one elongated cell, leaf margin glabrate; 3b.i = trichomes flattened in transverse section, adpressed, consisting of one elongated cell, leaf margin not glabrate; 3b.ii = trichomes flattened in transverse section, adpressed, consisting of more than one elongated cell, leaf margin not glabrate; 4a = leaves glabrous, trichomes on stems; 4b = leaves and stems glabrous

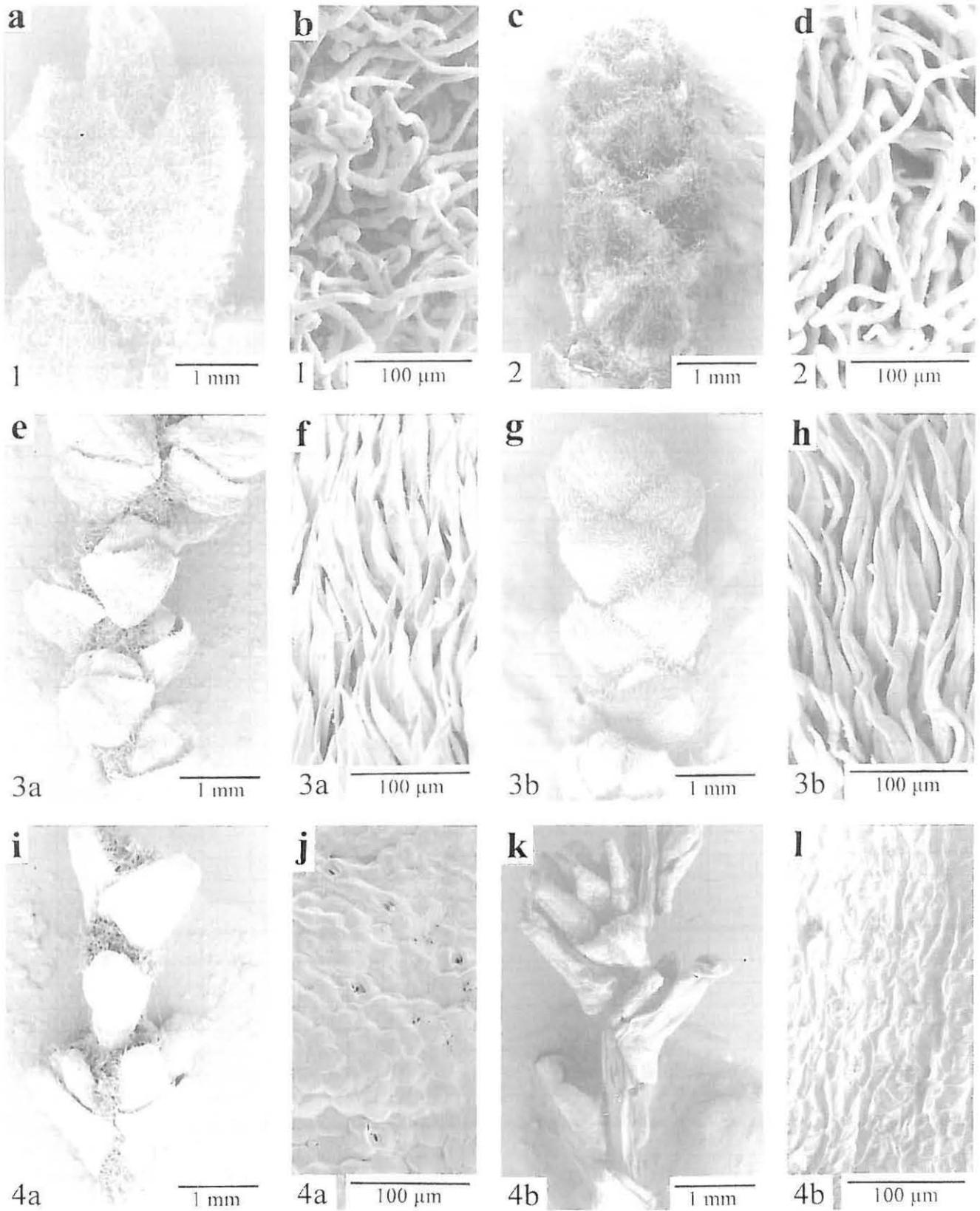


Figure 3: Indumentum types. **a and b** Indumentum Type 1. **c and d** Indumentum Type 2. **e and f** Indumentum Type 3a. **g and h** Indumentum Type 3b. **i and j** Indumentum Type 4a. **k and l** Indumentum Type 4b

of the investigated species into four groups (Table 2). One of the four indumentum types can be further subdivided according to the area of the leaf covered by the trichomes, and the number of elongated cells in the trichome.

Key to indumentum types

- Trichomes long, round in transverse section, entangled *Indumentum Type 1*
- Trichomes round to flattened in transverse section, slightly adpressed to almost entangled.....*Indumentum Type 2*
- Trichomes flattened in transverse section, adpressed.....*Indumentum Type 3*
 - Leaf margin* glabrate.....*Type 3a*
 - Trichomes consisting of one elongated cell..*Type 3a.i*
 - Trichomes consisting of more than one elongated cell*Type 3a.ii*
 - Leaf margin not glabrate.....*Type 3b*
 - Trichomes consisting of one elongated cell.....*Type 3b.i*
 - Trichomes consisting of more than one elongated cell*Type 3b.ii*
- Trichomes absent, at least on leaves....*Indumentum Type 4*
 - Leaves glabrous; trichomes present on stems.....*Type 4a*
 - Leaves and stems glabrous.....*Type 4b*

* With leaf margin is meant the marginal zone consisting of an area ± 300–500µm wide. This usually constitutes that part of the leaf margin zone where the palisade mesophyll and bundle sheath layers are absent.

Description of Indumentum Types

Indumentum type 1

Trichomes non-glandular, simple, multicellular, uniseriate; long, round in transverse section, entangled, (195–) 290–595 (–765)µm long; basal cell short, elongated cells 1–3.

Species possessing Indumentum Type 1 (Leaf Type in brackets)

- S. araneosa* (H+) *S. zeyheri* (H+)

Indumentum type 2

Trichomes non-glandular, simple, multicellular, uniseriate; long to intermediate length, round to flattened in transverse section, slightly adpressed to almost entangled, (120–) 150–440 (–750)µm long; basal cell short, elongated cells 1–3; leaf margin sometimes glabrate, fringed; trichomes sometimes easily rubbed off.

Species possessing Indumentum Type 2 (Leaf Type in brackets)

- S. decussata* (H-) *S. gemmata* (H-) *S. sericata* (H+)
S. dinteri (H-) *S. scopiformis* (H+)

Indumentum type 3a.ii

Trichomes non-glandular, simple, multicellular, uniseriate; long to intermediate length, flattened in transverse section, adpressed, (95–) 120–275 (–380)µm long; basal cell short, elongated cells 1–2; leaf margin glabrate, sometimes

fringed; trichomes sometimes easily rubbed off.

Species possessing Indumentum Type 3a.ii (Leaf Type in brackets)

- S. aphylla* (H+) *S. cauliflora* (H-) *S. ceresica* (H+)

Indumentum type 3b.i

Trichomes non-glandular, simple, multicellular, uniseriate; long to very short, flattened in transverse section, adpressed, (80–) 120–220 (–330)µm long; basal cell short, elongated cell one; leaf margin sometimes strongly fringed; trichomes sometimes easily rubbed off.

Species possessing Indumentum Type 3b.i (Leaf Type in brackets)

- S. albida* (H+) *S. melanantha* (H-) *S. robinsonii* (H+)
S. etoshensis (H+) *S. microtricha* (H+) *S. tuberculata* (H+)
S. giessii (H+) *S. okaukuejensis* (H+) *S. tuberculatiformis* (H+)
S. huabica (H+) *S. patentipilosa* (H+) *S. warmbadica* (H+)
S. koichabica (H+) *S. rabieana* (H+)

Indumentum type 3b.ii

Trichomes non-glandular, simple, multicellular, uniseriate; intermediate length, flattened in transverse section, adpressed, (153–) 175–215 (–238)µm long; basal cell short, elongated cells two; trichomes easily rubbed off.

Species possessing Indumentum Type 3b.ii (Leaf Type in brackets)

- S. acocksii* (H+)

Indumentum type 4a

Mature leaves glabrous, sometimes fringed, sometimes with trichomes on young leaves and flowers, lost during maturing; trichomes on stem long, round to flattened in transverse section, sometimes entangled.

Species possessing Indumentum Type 4a (Leaf Type in brackets)

- S. aellenii* (H-) *S. gemmifera* (H+) *S. inaperta* (H-)
S. apterygea (H+) *S. glabra* (H-) *S. minutifolia* (H-)
S. dealata (H+) *S. glabrescens* (H+) *S. seminuda* (H-)
S. denudata (H-) *S. humifusa* (H+) *S. smithii* (H-)
S. exalata (H+)

Indumentum type 4b

Leaves and stem glabrous.

Species possessing Indumentum Type 4b (Leaf Type in brackets)

- S. calluna* (H-)

Discussion and additional observations

The genus *Salsola* possesses a number of adaptive leaf characters that correspond to the xerophytic habitat occupied by these plants in southern Africa. All these characters are suspected to minimise transpiration and thus prevent excessive water loss in an arid environment, and also to protect the plant's vital tissues from extreme heat. Leaves of the

investigated species are all terete and very small. In most species leaves are between 1–2mm in length, often with the same or slightly smaller width. Leaves are succulent and can be between 0.5–1.5mm thick. This gives the leaves a high surface to volume ratio, which is one of the most prevalent xeromorphic characters (Esau 1977, Metcalfe and Chalk 1983, Fahn and Cutler 1992).

Corresponding with the findings of other researchers (Solereder 1908, Esau 1977, Metcalfe and Chalk 1983), *Salsola* leaves have a very thick mesophyll. Palisade mesophyll is quite well developed in most species. The spongy mesophyll is not typical, but is rather characterised by the absence of intercellular spaces and comprises of centrally placed aqueous tissue, enclosing the main vascular bundle and its branches.

An important aspect that has been highlighted by this study is the exact anatomical structure of the leaves in southern African members of *Salsola*. Typical Salsoloid-type Kranz-anatomy (Carolin *et al.* 1975) was not found in the investigated material. Instead, all taxa show a variation on this type of Kranz-anatomy. Leaves are inversely-dorsiventral, with the palisade mesophyll and bundle sheath layer, and its associated networks of secondary vascular bundles, only being present abaxially (Figures 1 and 2). The reason for this configuration may be the shape of the leaves. The apex of the leaf in *Salsola* species from the northern hemisphere, for example *S. kali*, is usually elongated into a spine that is exposed to the environment on all sides. In a transverse section through one of these spines, the palisade mesophyll and bundle sheath layers form a continuous layer around the leaf. Southern African *Salsola* species do not have such extremely elongated leaves, but leaves typically have a short rounded apex (Figure 1). Leaves are also very densely packed, with their adaxial epidermis adpressed against the stem, thus covering the branches almost completely. This may be the reason for the adaxial absence of the palisade mesophyll and bundle sheath layers. Some leaves of a few indigenous species tend to have an apex that is somewhat elongated, but not as much as in the northern hemisphere species. In a transverse section through the apex of such a leaf, the palisade mesophyll and bundle sheath layers form a continuous layer around the leaf, but it is not as pronounced as in, for instance, *S. kali*.

Epidermal cells of the investigated species are generally small; those of the adaxial epidermis being smaller than those of the abaxial epidermis. The adaxial epidermis is on average $\pm 10\mu\text{m}$ thinner than the abaxial one. Epidermal cell walls are notably thickened, with the outer periclinal cell walls more often thicker than the inner periclinal or anticlinal cell walls. These are common features of xerophytic plants (Metcalfe and Chalk 1983).

The adaxial cuticle is almost always thinner than the abaxial one. Adaxially the cuticle is mostly less than $1\mu\text{m}$ thick, while abaxially it averages $3\mu\text{m}$, exceeding $4\mu\text{m}$ in some species. One would expect a thick cuticle in xerophytic plants such as *Salsola*, but cuticle thickness can be an extremely variable character (Esau 1977, Metcalfe and Chalk 1983, Fahn and Cutler 1992) and the foliage cuticle rarely attains a considerable thickness in the Chenopodiaceae (Solereder 1908). The thin cuticle of these

Salsola species may be due to an effective chemical composition that limits cuticular transpiration just as effectively as a thick cuticle (Mèrida *et al.* 1981, Jordaan and Kruger 1992, 1998). The formation of thin, effective cuticles instead of thick ones can be a way of conserving energy during growth (Jordaan and Kruger 1998).

All the investigated species have hypostomatic leaves with paracytic stomata. As the adaxial epidermis is adpressed against the stem and not readily in contact with the atmosphere, gas exchange through this surface would be extremely difficult. This may be the reason for the total absence of stomata on the adaxial surface. Stomata are abaxially abundant in most species, sometimes with a thick cuticle, and only occur in that area where the palisade mesophyll and bundle sheath layers are present internally. These two layers are necessary for photosynthesis and thus rely on proper gas exchange. The aqueous mesophyll subtending the epidermis of the leaf margins is mostly storage tissue and does not depend on gas exchange. Therefore, this area of the leaf does not need stomata. This explains the pattern of distribution of stomata on the abaxial leaf surface.

In xerophytes one would expect stomata to be sunken below the surface to help prevent water loss (Solereder 1908), but especially in species with a very dense covering of trichomes, this is not always necessary. In some investigated *Salsola* species the stomata are sunken below the epidermis, but mostly the inner periclinal walls of the epidermal and guard cells are aligned. In the latter case, the stomata still remain below the general surface of the leaf, because the epidermal layer is thicker than the anticlinal dimensions of the stomata. In a few species the stomata are situated at the epidermal surface and not sunken at all. Guard cells are parallel to one another and the stomatal pores are arranged transversely to the median vein of the leaf. This corresponds to an important character found by other researchers in members of the Chenopodiaceae with terete leaves (Solereder 1908).

The presence of a hypodermis is common amongst xerophytic plants (Esau 1977). An abaxial hypodermal layer containing prismatic crystals is present in all species investigated. This hypodermis is a common feature of many members of the Chenopodiaceae, as well as other *Salsola* species (Solereder 1908, Carolin *et al.* 1975, Carraro *et al.* 1993, Patrignani *et al.* 1993). In addition to the always present abaxial hypodermis, some investigated species also possess an adaxial hypodermis. Cell walls of the adaxial hypodermis are lignified and the layer is sclerenchymatous. This might act as a strengthening tissue to help protect the leaves against the injurious effects of wilting (Esau 1977, Metcalfe and Chalk 1983, Tootill 1984) or to protect the leaf surface against herbivorous insects. Similarly, the abundance of crystals (presumable calcium oxalate) present in the adaxial as well as the abaxial hypodermis, might serve as a protective measure against insects and other small herbivores (Solereder 1908). *Salsola* species are readily grazed by a large number of animals. It has been stated that the presence or absence of a hypodermis appears to have no taxonomic significance in the Chenopodiaceae (Carolin *et al.* 1975), a statement not supported by our observations. The

full taxonomic significance of the adaxial hypodermis layer in *Salsola* is not yet clear, but it might be correlated to some other morphological or even ecological character.

The presence or absence of an adaxial hypodermis has been used to divide the investigated species into two main groups (Table 2). Species displaying Leaf Type H+ are by far the larger of the two groups, comprising 28 of the 43 investigated indigenous species. Of these 28 species all but one, *S. exalata*, belong to subsection *Caroxylon* (plants with alternate phyllotaxis). The remaining 15 investigated native species possess Leaf Type H-. The latter leaf type is present in both subsections *Caroxylon* and *Tetragonae* (plants with opposite phyllotaxis). Seven of the eight investigated species in subsection *Tetragonae*, however, possess Leaf Type H-. The only exception is *S. exalata* which possesses Leaf Type H+. This weak association between leaf type and subsection may well be significant. However, work needs to be done on the remaining species not covered by this study to establish their leaf type, especially in subsection *Tetragonae*. The fact that *S. exalata* is the only species in this subsection with Leaf Type H+ raises questions about its position within the subsection. This certainly calls for a thorough investigation of this species, starting with the phyllotaxis, as this is the main character used by Botschantzev to delimit the existing subsections.

Of the 43 native species investigated, only 14 as well as the alien *S. kali*, have glabrous mature leaves (Table 2). Most of these glabrous species do, however, have trichomes on their young developing leaves and/or flowers. This can be attributed to the fact that the young developing parts are in greater need of protection and that trichomes fulfil this protective role (Uphoff 1962). These trichomes are lost during or shortly after maturation of the leaves (Uphoff 1962, Metcalfe and Chalk 1979).

Trichomes are only present on the abaxial leaf surface and completely absent from the adaxial one (Figure 2). There are a number of other xeromorphic plants where trichomes occur only, or are much more abundant, on the abaxial leaf surface (Fahn 1986). This phenomenon may have various explanations, as well as a number of benefits. In *Salsola* it can easily be explained by the fact that the adaxial leaf surface is adpressed against the stem and thus sufficiently protected.

In some species (those with Indumentum Type 3a), trichomes mostly occur where the palisade mesophyll and bundle sheath layers are present internally and not on the leaf margins subtended only by aqueous mesophyll (Figures 2 and 3). Stomata of all species also occur in this area only. The palisade mesophyll and bundle sheath are the most vital tissues of the leaf for photosynthesis and thus need to be protected. Aqueous mesophyll does not contain chlorophyll and is perhaps not in such great need of protection as the two chlorophyll-containing layers. Trichomes provide protection to the subtending tissue against the damaging effect of insolation and to prevent extreme water loss (Uphoff 1962, Esau 1977, Metcalfe and Chalk 1979), but is costly to produce. Thus plants can conserve energy by not producing a dense trichome covering in areas where it is not needed, such as the leaf margins in this case. This can explain the glabrate nature of the leaf margins of these species.

All trichomes in the investigated species are non-glandular, simple, multicellular and uniseriate. Trichomes are seated on a prominent basal epidermal cell and contain a terminal portion consisting of one to three elongated cells. This corresponds to the commonly found trichome types in the Chenopodiaceae and Salsoleae (Solereder 1908, Uphoff 1962, Metcalfe and Chalk 1979). The majority of species (21), especially those with shorter trichomes, only have one elongated cell. Most species (22) possess flattened, adpressed trichomes forming a smooth surface. Only a small number of species have trichomes that are entangled (two species) or only slightly adpressed to almost entangled (five species).

The two largest indumentum types are Type 3b.i with 11 species and Type 4a with 14 species. The other indumentum types all consist of between one and six species. There is a weak association between indumentum type and subsection. Indumentum types are fairly evenly distributed in subsection *Caroxylon*, with all types occurring in this subsection. The investigated species of this subsection comprises two species with Indumentum Type 1, four species with Indumentum Type 2, five species with Indumentum Type 3a.i, three species with Indumentum Type 3a.ii, 11 species with Indumentum Type 3b.i, one species with Indumentum Type 3b.ii, eight species with Indumentum Type 4a and one species with Indumentum Type 4b. In subsection *Tetragonae* Indumentum Types 1, 3a.ii, 3b.i, 3b.ii and 4b were not found. This smaller subsection contains one species with Indumentum Type 2, one species with Indumentum Type 3a.i and six species with Indumentum Type 4a. An association between indumentum type and subsection can, therefore, be most clearly seen in the two largest indumentum types. Indumentum type 3b is entirely restricted to subsection *Caroxylon*, whereas six of the eight species investigated in subsection *Tetragonae* possess Indumentum Type 4a. The greatest majority of species in the latter subsection are thus glabrous. However, the indumentum of the species in subsection *Caroxylon* varies from long entangled trichomes, through short adpressed trichomes to completely glabrous plants.

Noteworthy is the weak association between leaf type and indumentum type. Only six of the 28 investigated species with trichomes possess Leaf Type H-, whereas nine of the 15 glabrous species possess Leaf Type H-. The six species with Leaf Type H- that possess trichomes mostly have glabrate leaf margins, an indumentum that is not very dense or trichomes that are rubbed off easily. Both species with Indumentum Type 1, that appears to be a very dense indumentum, possess Leaf Type H+. Species with Indumentum Type 2 are more or less evenly distributed between Leaf Type H+ (two species) and Leaf Type H- (three species). This indumentum type can be seen as an intermediate type between the long entangled trichomes of Indumentum Type 1 and the adpressed trichomes of Indumentum Type 3. In Indumentum Type 3 there are a small number of species with Leaf Type H- (only three out of a total of 19 species). These three species are *S. henriciae* (3a.i) and *S. cauliflora* (3a.ii), which are two of the five species with Indumentum Type 3a, and *S. melanantha* (3b.i), comprising one out of 14 species with Indumentum Type 3b. This difference in indumentum

density between the two leaf types is clearly more pronounced in species with Indumentum Type 3b, where leaf margins are not glabrate and the overall trichome covering thus denser, than in Indumentum Type 3a. Of the 14 indigenous glabrous species only five, namely *S. apterygea*, *S. dealata*, *S. exalata*, *S. gemmifera* and *S. glabrescens*, possess Leaf Type H+. Five of the nine glabrous species with Leaf Type H- belong to the subsection *Tetragonae*. Note that the only species in subsection *Tetragonae* with Leaf Type H+, *S. exalata*, also has glabrous leaves. This further complicates the question around the taxonomic position of this species. Other than the leaf type, the indumentum type supports the position of the species within the subsection. This all contributes to a generalised observation that those species possessing an adaxial hypodermis tend to have a denser covering of trichomes than those species without an adaxial hypodermis. This might be taxonomically very useful if an association can be found between leaf type and some other morphological or ecological character of the genus.

Leaf and indumentum type seem to be evenly distributed throughout the geographical range of the genus. No clear correlation could be found during this study between these types and any other character. However, the limited amount of material used did not permit a thorough exploration of possible associations. Further investigations should focus on this aspect. Possible characters to be taken into account are geographical distribution of species in terms of climate, soil type, geology and topography and vegetation type; other anatomical characters of the leaves, flowers and fruit; and possibly even chemical constituents, palatability and the extent to which each species is utilised by livestock.

The main aim of this study was to contribute towards the systematics of the genus *Salsola* in southern Africa and in particular to find additional characters that may facilitate the identification of the different species. During this study the leaf anatomy and macro-morphology proved to be very helpful for dividing the section *Caroxylon* into groups. In this respect the presence or absence of the adaxial hypodermis may be an important character to assist in the grouping and identification of species. It is unfortunately not very easily observed without the aid of at least hand sections or epidermal peels and simple staining techniques. It could, nevertheless, be used as the basis of an identification system, especially if it can be correlated with some other more visible characters. The possible existence of such characters and their potential taxonomic significance, calls for further investigation.

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